State factor relationships of dissolved organic carbon and nitrogen losses from unpolluted temperate forest watersheds

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[1] We sampled 100 unpolluted, old-growth forested watersheds, divided among 13 separate study areas over 5 years in temperate southern Chile and Argentina, to evaluate relationships among dominant soil-forming state factors and dissolved carbon and nitrogen concentrations in watershed streams. These watersheds provide a unique opportunity to examine broad-scale controls over carbon (C) and nitrogen (N) biogeochemistry in the absence of significant human disturbance from chronic N deposition and land use change. Variations in the ratio dissolved organic carbon (DOC) to nitrogen (DON) in watershed streams differed by underlying soil parent material, with average C:N = 29 for watersheds underlain by volcanic ash and basalt versus C:N = 73 for sedimentary and metamorphic parent materials, consistent with stronger adsorption of low C:N hydrophobic materials by amorphous clays commonly associated with volcanic ash and basalt weathering. Mean annual precipitation was related positively to variations in both DOC (range: 0.2–9.7 mg C/L) and DON (range: 0.008–0.135 mg N/L) across study areas, suggesting that variations in water volume and concentration may act synergistically to influence C and N losses across dry to wet gradients in these forest ecosystems. Dominance of vegetation by broadleaf versus coniferous trees had negligible effects on organic C and N concentrations in comparison to abiotic factors. We conclude that precipitation volume and soil parent material are important controls over chemical losses of dissolved organic C and N from unpolluted temperate forest watersheds. Our results raise the possibility that biotic imprints on watershed C and N losses may be less pronounced in naturally N-poor forests than in areas impacted by land use change and chronic N deposition.

1. Introduction

[2] Understanding patterns of carbon (C) and nitrogen (N) loss is of fundamental interest in studies of watershed biogeochemistry [*Vitousek and Reiners*, 1975]. Strong linkages between these two biogeochemically important elements can arise owing to widespread nitrogen limitation of plant growth in temperate forests [*Vitousek and Howarth*, 1991], and because of stoichiometric couplings of the elements in plant and microbial biomass [*Melillo et al.*, 1982]. Recent increases in atmospheric CO_2 and nitrogen deposition across many regions has heightened interest in understanding factors that control carbon and nitrogen losses across forested watersheds [*Huntington*, 2005; *Goodale et al.*, 2005]. However, since all terrestrial ecosystems are subject to similar changes in the well-mixed atmospheric CO_2 pool, it has been to difficult to evaluate how patterns of hydrologic C and N loss from forests might differ across gradients of CO_2 impacts. In contrast, experimental and comparative studies often suggest that interactions between ecosystem N status and atmospheric N deposition can explain a large portion of variations in patterns of dissolved N export across watersheds [*Gunderson et al.*, 1998a]. At the regional and local scale, variations in nitrate loss can be related to variations in forest succession [*Vitousek and Reiners*, 1975; *Goodale et al.*, 2000], forest species composition [*Lovett et al.*, 2002], litter and soil C:N [*Gunderson et al.*, 1998b], climatic variation and events [*Aber and Driscoll*, 1997; *Houlton et al.*, 2003] and biotic [*Eshelman et al.*, 1998] events.

[3] Information on controls over dissolved organic carbon (DOC) and nitrogen (DON) are less well understood. The relative dominance of DON over inorganic forms of N in hydrologic losses from unpolluted, old-growth temperate forests is generally attributed to low rates of atmospheric N input relative to overall loss rates [*Sollins et al.*, 1980; *Hedin et al.*, 1995; *Perakis and Hedin*, 2002]. Wetlands may further modify this pattern and increase the importance of DON exports for regions with significant anthropogenic N inputs [*Pellerin et al.*, 2004]. However, understanding of

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the factors that control variations in the ratios of DOC:DON across watersheds in natural landscapes remains elusive. This information can however have important implications for understanding the degree of C:N couplings in terrestrial ecosystems, and how such couplings influence ecosystem-level patterns of nutrient limitation [*Schimel et al.*, 1997], the response to elevated CO_2 and temperature [*Rastetter et al.*, 2005], and the quality and quantity of dissolved organic matter delivered to downstream aquatic ecosystems [*Brookshire et al.*, 2005].

[4] We here analyze variations in dissolved carbon and nitrogen forms as a function of primary state factors (climate, organisms, parent material, time) thought to control soil and ecosystem development. From previous studies, we anticipated that variations in DOC:DON ratio in stream water would predict concentration losses of NO_3^- from watershed streams [e.g., *Goodale et al.*, 2000]. Given climatic control over global C and N in soil organic matter [*Post et al.*, 1982, 1985], and the close relationship between soil C:N and watershed DOC:DON flux [*Aitkenhead and McDowell*, 2000], we also expected that climate variables may be an important predictor of DOC:DON loss ratios. Finally, owing to possible shifts in N limitation across gradients of soil age, we predicted greater concentration losses of inorganic N as nitrate from ecosystem with older soils [*Hedin et al.*, 2003].

2. Methods

2.1. Study Watersheds

[5] Our study considered small (<~100 ha) old-growth forested watersheds (n = 100) located between 40 and 54 degrees south latitude in Chile and Argentina, South America. Rates of N deposition across this region are among lowest in the world, owing to prevailing weather patterns from the Pacific Ocean to the west [*Holland et al.*, 1999]. Sample watersheds were grouped into 13 study areas representing unique combinations in the principal state factors of soil and ecosystem development [*Jenny*, 1941]. Sample watersheds within a study area were contiguous small headwater streams, sufficiently local to share common features of climate, vegetation, topography, parent material, and time. Sampling occurred by backpacking into roadless areas, or by small road access and hiking into old-growth forest. All study areas lack a significant component of vascular N fixing plants [*Hoffmann*, 1982]. Only individual small streams were sampled <2 m bank full width, under full forest canopy.

[6] Our study watersheds exhibited wide variations in the principal state factors (climate, organisms, relief, parent material, time) thought to control soil and ecosystem development, details of which are presented elsewhere [*Perakis and Hedin*, 2002]. Briefly, we characterized these variations as follows. We used mean annual precipitation (MAT range = 500–5840 mm) and mean annual temperature (MAP range = 4°–11°C) as component variables of the climate factor. Organisms were classified as to whether coniferous and broadleaf species co-occurred as canopy dominants (n = 8), or whether broadleaf species dominated (n = 5). Geological parent material was classified as either part of the mineralogically distinct Andic soils that are common in the Pacific rim, or differing from such soils.

Our reasons for this grouping was that Andic soils develop from the weathering of volcanic ash and some igneous rocks (n = 7 study areas occurring on field-verified tephra and igneous parent materials, Table 1), characterized by an abundance of poorly crystalline amorphous clays with high capacity for organic matter sorption and protection relative to crystalline clays typical of non-Andic soils [*Percival et al.*, 2000]. More detailed soil taxonomic information is not available for these sites, but rudimentary excavations and roadcuts revealed well-developed soils to >60 cm depth in all sites, except the tephra-dominated Antillanca which contained a buried organic horizon at approximately 30 cm depth. We classified *time* as a categorical variable, and considered young study areas as developing after recent disturbance (<4 kyr, n = 2 areas), intermediate age areas as developing after the last major southern glaciation (<18 kyr, n = 7 areas), and old areas as escaping the last major glaciation (>22.5 kyr, n = 4 areas). All areas were located in montane regions, and therefore did not include topography as a variable in our analysis. Of the 13 study areas, nine were separated geographically by up to thousands of kilometers, and the remaining four were located in two geographic regions, distinguished from one another by contrasting vegetation. Our approach in sampling across these wide state-factor variations seeks to investigate macroscopic variations at large scales that are not evident in more traditional and intensive temporal studies of many fewer gauged watersheds.

2.2. Sampling and Analysis

[7] We sampled multiple watersheds (n = 2–14 streams per area) within each of the 13 study areas. Differences in numbers of watersheds sampled among study areas reflect logistical difficulties in accessing roadless watersheds. Each study area was visited once, with the year of sampling (1994, 1995, 1997, 1998, 1999) varying according to the sampling campaign, although all areas were sampled in relatively dry austral summer months December through March. Aggregate patterns of hydrologic C and N loss from all our study areas have been previously examined as part of a broad-scale comparison of nutrient loss patterns against more N-polluted watersheds in the Northern Hemisphere [*Perakis and Hedin*, 2002]. Data from individual study areas are presented in Table 1.

[8] Two replicate samples were collected from each watershed per sampling event using clean 60 mL polyethylene syringes, and were filtered in the field through rinsed Gelman A/E glass fiber filters into clean 60 mL polyethylene bottles. One replicate was immediately preserved with 0.2 mL $CHCl_3$ to prevent biological activity, and all samples were kept cool (<10°C) and dark until analysis at Cornell University, Ithaca, New York, generally within 2 weeks of collection. NH_4^+ was analyzed by Alpkem continuous flow colorimetry, NO_3^- by Dionex ion chromatography, total dissolved nitrogen by colorimetry as NO_3^- following high-temperature persulfate digestion, and DOC by Shimadzu high-temperature platinum combustion [*Hedin et al.*, 1995]. DON was calculated as total dissolved N minus NH_4^+-N and NO_3^--N. There were no significant autocorrelations among any state factor variables considered in this analysis, so we used reverse stepwise regression to examine relationships between state-factors and patterns of watershed nitrogen and

Table 1. Dissolved Carbon and Nitrogen Concentrations in Watershed Streams[a]

Study Area	Watersheds Sampled	MAP, mm	MAT, °C	Vegetation	Parent Material	NO_3^-, µg N/L	NH_4^+, µg N/L	NO_3^--N: NH_4^+-N	DIN, µg N/L	DON, µg N/L	TDN, µg N/L	DOC, mg C/L	DOC: DON
Piuchue mixed	10	5840	6	mixed	PC	0.11 (0.03)	3.65 (0.42)	0.02 (0.01)	3.8 (0.4)	126.4 (6.8)	130.2 (7.0)	8.1 (0.5)	77 (2.2)
Piuchue conifer	2	5840	6	conifer	PC	0.12 (0.07)	5.43 (0.53)	0.02 (0.01)	5.6 (0.5)	124.6 (5.5)	130.2 (5.9)	9.7 (0.4)	81 (0.2)
Puyehue	11	3600	9	mixed	T	0.91 (0.24)	4.33 (1.02)	0.21 (0.05)	5.2 (1.2)	134.6 (18.5)	139.8 (18.6)	4.3 (0.4)	21 (4.8)
Cordillera Pelada	13	4000	8	mixed	PC	0.70 (0.29)	4.59 (0.86)	0.04 (0.05)	5.3 (1.0)	76.0 (7.6)	81.3 (7.8)	5.0 (0.4)	70 (5.8)
Lago Los Cesares	8	1500	7	mixed	T, GL	0.12 (0.04)	3.73 (0.78)	0.03 (0.02)	3.9 (0.8)	9.9 (3.2)	13.1 (3.0)	0.3 (0.1)	15 (6.0)
Southern Chiloe	5	2500	8	mixed	GL	2.63 (0.90)	9.85 (2.13)	0.38 (0.13)	12.5 (1.7)	111.1 (23.1)	123.6 (24.0)	6.1 (1.0)	49 (4.8)
Lago La Plata	9	770	7	mixed	T, GL	1.06 (1.00)	2.82 (0.55)	0.03 (0.19)	3.9 (1.4)	25.7 (4.4)	29.6 (4.2)	1.0 (0.2)	54 (4.4)
Senda Kruger	5	1200	7	deciduous	T, I	0.60 (0.53)	2.71 (0.35)	0.03 (0.19)	3.3 (0.6)	7.9 (2.3)	11.2 (2.5)	0.4 (0.1)	18 (19.9)
Lago Futalaufquen	14	1200	9	conifer	T, I	0.37 (0.17)	3.62 (0.68)	0.08 (0.06)	4.0 (0.7)	11.4 (3.6)	14.1 (3.9)	0.2 (0.1)	22 (7.0)
Alerce Andino	8	4000	7	mixed	I	7.25 (3.50)	11.32 (3.20)	0.27 (0.38)	18.6 (4.9)	34.6 (7.1)	53.2 (7.2)	2.6 (0.3)	47 (17.0)
Hueicolla	7	2500	11	mixed	PC	7.70 (2.29)	7.99 (1.91)	0.74 (0.26)	15.7 (3.8)	62.2 (16.0)	77.9 (12.8)	2.4 (0.3)	66 (57.2)
Tierra del Fuego	2	500	4	deciduous	GL	0.02 (0.00)	0.50 (0.00)	0.04 (0.00)	0.5 (0.0)	19.0 (0.50)	19.5 (0.5)	0.5 (0.1)	94 (8.5)
Antillanca	6	5400	4	deciduous	T	2.82 (1.76)	2.90 (0.35)	0.12 (0.53)	5.7 (1.9)	18.1 (10.8)	20.6 (10.9)	2.1 (0.3)	26 (95.7)

[a]Concentrations are calculated as arithmetic means, with standard errors in parentheses. Abbreviations for geological parent materials are: PC, pre-Cambrian mica-shists; GL, glacial till; T, tephra; and I, igneous basalt, granite, andesite.

carbon loss across the 13 study areas. Regressions were conducted using SYSTAT version 11.2 (SYSTAT, Inc., Richmond, California), with variables entered and removed at $p = 0.15$, and statistical significance set to $p < 0.05$.

3. Results and Discussion

[9] We found much wider variations in stream water concentrations of DON than DIN draining watersheds (Table 1), contrary to findings from most regional studies of polluted temperate forest watersheds [*Goodale et al.*, 2000; *Lovett et al.*, 2000; *Lewis*, 2002; *Binkley et al.*, 2004]. We also found that state factor attributes were more effective in predicting concentration variations for organic than inorganic forms of nutrients. In particular, mean annual precipitation (MAP) correlated with concentrations of DOC and DON in watershed streams, but did not correlate with dissolved inorganic N species or ratios (Table 2). Correlation analysis showed that MAP explained 64% of the variation in DON across areas, and together with parent material predicted 79% of the variation in watershed DOC. The mechanism(s) relating precipitation to concentrations of DOC and DON in stream waters is likely to be similar for both solutes, since the functional charge characteristics that control the bulk transport of dissolved organic matter (DOM) in soils are considered much more important than behaviors of distinct C or N containing functional groups [*Qualls and Haines*, 1991]. The close correlation observed between concentrations of DOC and DON in watershed losses [*Perakis and Hedin*, 2002] provides general support for this idea, and suggests a common origin for bulk DOC and DON. Other studies have found soil C:N correlates with watershed DOC and DON flux [*Aitkenhead and McDowell*, 2000; *Hood et al.*, 2003; *Aitkenhead-Peterson et al.*, 2005], yet all state factors except time influence soil C:N [see *Aitkenhead-Peterson et al.*, 2005], making it difficult to resolve which state factor(s) ultimately are most important in relating soil C:N to dissolved organic matter (DOM) export. Likewise, we cannot identify conclusively which specific mechanism(s) may relate precipitation to DOC and DON variations across our study areas. At broad scales, pools of soil C and N increase with precipitation, particularly in mesic to wet regions [*Post et al.*, 1982, 1985], which may increase the availability of substrates for DOM loss. High precipitation rates may also increase water throughput and soil pore water velocity, especially in shallow soil horizons and stream sediments, thus lowering DOM sorption by reducing contact times between DOM and reactive mineral surfaces [*Kalbitz et al.*, 2000]. Over long periods, high precipitation inputs can also accelerate clay formation in mineral soil horizons [*Rai and Kittrick*, 1989], which may impede vertical water percolation through mineral soils, and enhance hydrologic short-circuiting of DOM from surface organic horizons to streams [*Hagedorn et al.*, 2000]. Regardless of the mechanism, our observed pattern of increasing DOC and DON concentrations with precipitation suggests that precipitation exerts strong control over biogeochemical C and N loss patterns across unpolluted temperate forest watersheds.

[10] Previous studies have reported conflicting variations in DON concentration in response to precipitation amount and/or watershed runoff; with both increases [e.g., *Arheimer*

Table 2. Results of Stepwise Regression of State Factors on Dissolved Nitrogen and Carbon Concentrations, and Ratios, in Small Watershed Streams[a]

Response Variable	Significant Terms in Final Model	r^2
NH_4^+	...	ns
NO_3^-	...	ns
NO_3^--N:NH_4^+-N	MAP, MAT, GEOL, TIME	0.79
DIN	...	ns
DON	MAP	0.64
TN	MAP, MAT, GEOL	0.76
% DON	GEOL	0.41
DOC	**MAP**, GEOL	0.79
DOC:DON	GEOL	0.78

[a]List of "terms in final model" are those contributing significantly at a minimum $p < 0.05$; terms in bold contribute at $p < 0.001$; "ns" indicates no significant predictive model.

et al., 1996; *McHale et al.*, 2000] and decreases [*Lewis et al.*, 1999; *Lewis*, 2002] observed for mesic to wet watersheds. Finer-scale seasonal [*Vanderbilt et al.*, 2002] and stormflow [*Wondzell and Swanson*, 1996] variations are also possible, which suggests that no single generalization appears to characterize DON concentration loss patterns across flows regimes for temperate forest watersheds. It is unlikely, however, that the broad patterns in our data are artifacts of our summer-based sampling regime. For example, while our grab sample concentrations of DON in Conifer Piuchue watersheds (125 μg N/L) are higher than 5-year volume-weighted mean DON measured biweekly from 1994–1999 (93 μg N/L), the long-term record of DON and DOC from these watersheds nevertheless exhibits little or no seasonal and hydrologic pattern [e.g., *Salmon et al.*, 2001] in comparison to the large concentration differences observed across geographic areas in our sampling (DON range: 8–135 μg N/L). In addition, snow was absent from all watersheds at the time of sampling, except for uppermost areas of high-elevation Antillanca watersheds, thus minimizing effects of snowmelt influence. The general pattern of increasing DON concentration that we observed across an order of magnitude range of precipitation volume (500 mm to 5840 mm MAP) across sample areas contrasts with results from a broad survey of temperate North American watersheds, where DON concentrations exhibited dilution with increasing discharge [*Lewis*, 2002]. Several factors unrelated to north-south differences may account for this discrepancy, including sampling scopes (continental versus subcontinental), DON concentration measures (annual weighted versus grab samples) and watershed areas (<10 ha versus >1800 ha). Our results agree however with individual small watershed studies from the Pacific Northwest of North America, where positive relationships between DON concentration and precipitation volume are common [*Edmonds et al.*, 1998; *Vanderbilt et al.*, 2002]. This similarity suggests that DON losses and N balances of Pacific temperate forests on both North and South American continents may be especially sensitive to future increases in precipitation expected to result from climate change in these regions.

[11] The development of characteristic C:N ratios in terrestrial and aquatic ecosystems is often attributed to the stoichiometric imprint of biological processes [*Sterner and Elser*, 2002]. Less emphasis is placed on abiotic or other environmental factors independent of their influence on biota. However, we found a strong and unexpected relationship between the DOC:DON of watershed solute loss and underlying parent material geology (Table 2). Most soil parent materials do not directly contribute N and/or DOC to solute chemistry, and, prior to weathering by water and biological agents, there is little opportunity for soil parent material to influence the C and N chemistry of water exiting small headwater basins. Likewise, geological control over watershed nitrate loss in polluted regions is considered to reflect bedrock weathering impacts on soil pH and fertility, not direct geological effects [*Williard et al.*, 2005]. For this analysis, we therefore considered weathering sequences that are typical of parent materials in Pacific montane environments, with focus on whether or not each parent material was considered broadly to promote the formation of Andic type soils. Both volcanic ejecta and some igneous rocks (e.g., basalt, rhyolite, dacite, andesite) form andic or andic-type soils throughout Pacific montane environments [*Takahashi and Shoji*, 2002].

[12] We show in Figure 1 that DOC:DON ratios of water draining forests developed on such andic-forming soil parent materials (mean and standard error of DOC:DON = 29, s.e. = 5.7, n = 6) was nearly half that observed for other soil parent material types (DOC:DON = 73 ± 6.2, n = 7, p < 0.001). This result implies that andic-type soil parent materials influences the DOC:DON of exported solutes in these watersheds, or that some other factor influences both the developmental sequence of andic soils and DOC:DON loss ratios. The greater adsorption capacity of Andic soils than other soil types for percolating dissolved organic matter [*Yano et al.*, 2005] offers one possible explanation. Hydrophobic compounds of high C:N are preferentially removed from soil water by soil clay surfaces [*Kalbitz et al.*, 2000], so that the strong adsorption properties of Andic soils might be expected to increase the proportion of N-rich
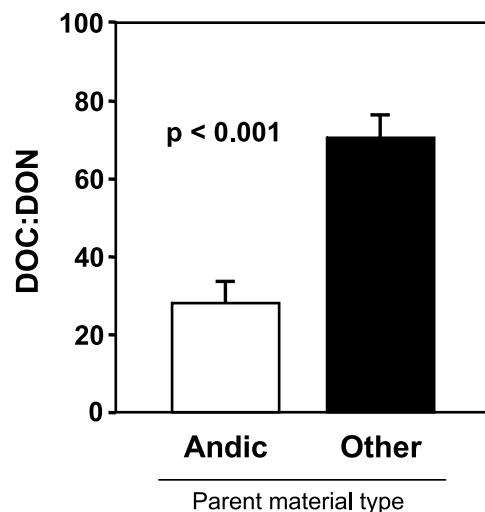

Figure 1. Comparison of DOC:DON ratios by mass of stream water draining watersheds underlain by soil parent materials leading to formation of Andic soils (n = 7) versus all other types (n = 8) of soil parent materials (see text for explanation). Data are mean and standard errors. Significance of t-test is shown.
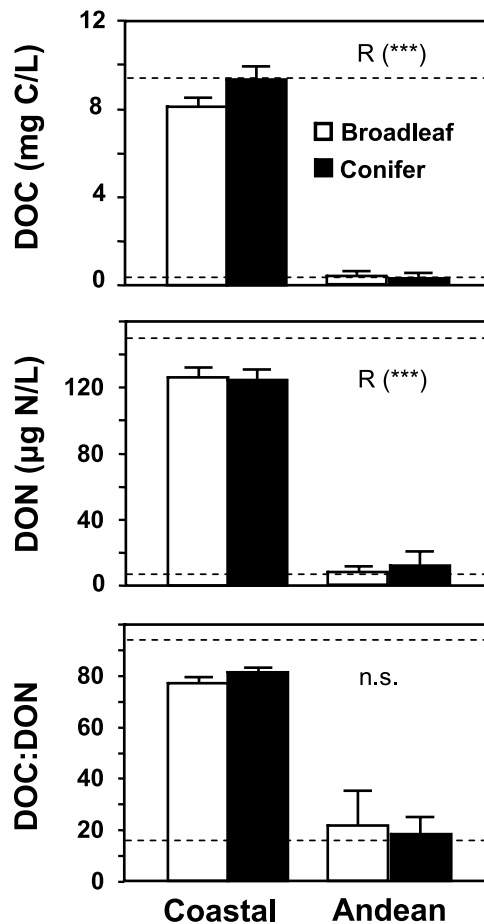
Figure 2. Comparison of DOC, DON, and DOC:DON in Coastal and Andean region streams dominated by either broadleaf (open bars) or coniferous (solid bars) vegetation. Data are mean and standard errors. In both regions, we located multiple (n = 2–9) watersheds <2 km apart. Coastal montane watersheds are cool (MAT = 6 C) and wet (MAP = 5840 mm), underlain by sedimentary parent material that escaped Holocene glaciation. Andean montane watersheds are warmer (MAT = 7–9 C) drier (MAP = 1200 mm), underlain by volcanic ejecta within the zone of Holocene glaciation. Dashed lines indicated maximum and minimum values recorded across all 13 study areas. Significant effects of vegetation type (V) and region (R) from two-way ANOVA are shown for each plot.

hydrophilic compounds remaining in solution, thus fostering loss of waters with low dissolved organic C:N. Alternatively, it is also possible that bulk mineral soil C:N, which correlates with DOC:DON of watershed export in some areas [*Hood et al.*, 2003; *Aitkenhead-Peterson et al.*, 2005], may be shaped ultimately by soil parent material variation across our study areas.

[13] We were surprised at the apparent lack of biotic effects on patterns and ratios of DOC and DON loss, as well as inorganic N loss, across watershed streams. Previous studies have suggested that biota can modify N cycling through soils via effects on the soluble pool of DON in soil [*Northup et al.*, 1995]. Laboratory studies have also shown that concentrations and ratios of soluble DOC and DON in

litter [*Magill and Aber*, 2000] and soils [*Smolander and Kitunen*, 2002] can differ between conifer and broadleaf trees, and we expected that such differences in biotic processing would be reflected in patterns of watershed C and N loss. However, we did not find such effects. In Figure 2 we show stream water DOC and DON chemistry from means of two sets of paired, adjacent conifer- versus broadleaf-dominated watersheds located in the Andean versus Coastal Cordilleras. Overall, concentrations and ratios of DOC and N species do not differ significantly between these contrasting biotic communities. In contrast, differences between Andean and Coastal subregions were significant for DOC and DON concentrations, and large but nonsignificant differences were observed for DOC:DON ratios as well. We conclude that the impact of tree species on patterns of N loss is small in naturally N-poor temperate watersheds when comparing within climatically, geologically, and developmentally similar regions.

[14] There is longstanding interest in the controls on inorganic N loss from forested watersheds. However, we did not find any relationships between state factors and concentrations of NO_3^- or NH_4^+ in watersheds streams. This was especially surprising considering the abundant evidence for biotic control over inorganic N loss patterns from polluted watersheds, including evidence that broadleaf versus coniferous classes [*Binkley et al.*, 2004] and even individual tree species [*Lovett et al.*, 2002] may influence watershed NO_3^- loss. With the possible of exception of regions where symbiotic N-fixing trees are important [e.g., *Compton et al.*, 2003], it appears that factors other than tree composition may regulate inorganic N losses in regions of low N input and availability. In-stream processing can also shape inorganic N loss patterns, but all of our watershed streams were small headwater systems with complete riparian canopy cover in old-growth forests, so that it is unclear whether and how in-stream processes may have differed across study areas. This absence of a clear biotic influence on inorganic N variations across our study areas is illustrated perhaps most clearly by the fact that all factors except biota contributed to resolving variations in NO_3^--N:NH_4^+-N ratios in watershed streams (Table 2).

[15] We expected that our characterization of biota as broadleaf versus coniferous vegetation would adequately reflect the mechanism(s) by which tree species influence N loss patterns. Tree species generally influence N availability through feedbacks associated with C:N stoichiometry, and associated specifically with patterns of leaf and litterfall chemistry, litter decomposition, and soil N mineralization [*Lovett et al.*, 2002]. Thus we included data from adjacent watersheds dominated either by the conifer *Fitzroya cuppresoides*, or by the broadleaf tree *Nothofagus nitida* [*Hedin et al.*, 1995]. Within these watersheds, the coniferous forests exhibit many characteristics of low N availability relative to the broadleaf forests, including significantly higher C:N in foliage, litter, and soil, as well as slower litter decomposition rates, lower net N mineralization, and lower percent nitrification [*Perez et al.*, 1991, 1998]. However, despite these differences in internal N dynamics, ratios of NO_3^--N:NH_4^+-N in streams of CP coniferous forests (ratio = 0.021) and MF broadleaf-dominated forests (ratio = 0.024) did not differ significantly. An analogous comparison of NO_3^--N:NH_4^+-N ratios in adjacent coniferous versus broad-

leaf dominated watersheds sampled in a drier Andean region shows similar results, with little difference in concentrations and ratios of C and N in hydrologic losses. Finally, it has been suggested that the DOC:DON ratio of watershed losses may reflect differences in long-term forest biogeochemical cycling, and higher NO_3^- losses have been associated with lower dissolved C:N ratios in northeast U.S. watersheds [*Goodale et al.*, 2000]. However, our study areas also failed to conform to this pattern ($r^2 < 0.2$), suggesting a marginal capacity for species effects on ecosystem C:N dynamics to influence inorganic N loss patterns. This is consistent with both experimental and observational studies that demonstrate greater effects by species on N cycling and nitrate availability under conditions of high N availability [*Wedin and Tilman*, 1990; *Lovett and Reuth*, 1999]. This provides support for the idea that the influence of species on watershed nitrate loss may be most pronounced where high N availability allows individual species characteristics to control ecosystem-level constraints on N conservation.

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